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Community structure of woody plants on islands along a bioclimatic gradient

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Abstract. Understanding patterns of community structure and the causes for their variation can be furthered by comparative biogeographic analyses of island biotas. We used woody plant data at the local scale to investigate variations in species rarity, alpha, beta, and gamma diversity within and between three islands from the oceanic archipelagoes of Azores, Canaries and Mascarene. We used standardized protocols to sample ten 50 m × 50 m forest plots in each of the three islands with contrasting climate and regional species pools: Terceira (Azores), Tenerife (Canaries), and Reunion (Mascarene Islands). Occupancy frequency distributions and species abundance distributions were used to investigate rarity. The partitioning of beta diversity in a distance-decay framework was used to test for spatial patterns of community composition. Rarity was much more pronounced in the highly diverse islands of Tenerife and Reunion than in the regionally poorer island of Terceira. The number of species rose faster with increasing sample area in both Tenerife and Reunion. The slope of the species rank abundance curve was steeper in Terceira whereas the richer island assemblages approached a lognormal model. Compositional changes according to spatial distance were mostly due to replacement of species in Terceira and Reunion. Our results point to important differences in the community structure of Terceira, which is the less diverse and temperate region in comparison to Tenerife and Reunion which are highly diverse.

Key words: Beta diversity partition, distance-decay, islands, rarity, species abundance distribution (SAD), species area relationship (SAR)

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Introduction

For a given taxonomic group, alpha diversity (i.e., š Z o } • d ‰] Œ •] Z v • š • U] À Œ •] š X Ç Z U • ‰ Ÿ š µ Œ v] ∀ ‰ Œ] } • u ‰ } •] Ÿ } w • P U u u] À Œ •] š X Ç Z } À Œ] ∀ o Œ • š Ç š Z Œ Œ P] } v o • Œ] + Œ v o š U] š v š Œ Œ o ‰ š (• ‰ Ÿ À Œ] Ÿ v } ‰] v µ u Œ v • } u ‰ } •] Ÿ } v P v Œ î ì í ð • d X Z • u • µ Œ } (•] À Œ Z] š Á Ç À Œ } Œ v U š } v •]] Œ + Œ • v ‰ } š (• ‰] Œ • Œ /] š • C l X v š Z • š Z Œ • Œ } Z v o Œ } • µ } v š Z • ‰ Ÿ] • š Œ] µ (Ÿ ‰ v] ~ ‰ Œ • v r • š v • µ š } š Z] 8 µ d š Ç š] v] • v š P v Œ] ì µ v v š ~ ' • š } õ õ ð / • v X š Š µ Ç š Z Œ o Ÿ] v • between alpha, beta, and gamma diversity with species µ v v] • } v o Œ v Œ o Ç] À] © v P Ÿ } ~ v X P X , Œ š š o î X í ï õ µ µ ô ò ó ï u Y µ š o î X í ñ • X š Z] • } v š Æ µ š Š } š Z } Œ o Ÿ] • ô o Ÿ] w •] u ‰ o] . G } Œ v • (µ v } • U v]] • o v } + • Œ Z ‰ } • •] o of performing studies that simultaneously account for À Œ] Ÿ] • v • À Œ • ‰ } š (• } u u µ v] • š š Œ Œ µ š µ v u o š Ç Z Œ o Ÿ } v • Z À ‰ Œ Œ] š š Z • ‰ Ÿ] • š Œ] µ Ÿ } v µ v v o U ‰ Z š U Ù P u u diversity.

t] š Z (Á Æ ‰ Ÿ } ‰ • U] • • • u o P v • temperate regions are less diverse than assemblages] v } u ‰ Œ š Œ } ‰ Œ P o] } v • Œ } Ã í ð • } š Z] v š Œ µ (• o } Œ] Z v ~ • o ‰] À Œ •] š Ç š] À Œ •] Y s µ Ç o X î ì í ñ • X] + Œ v] v • • ‰] community structure between species-poor temperate regions and species-rich tropical regions can arise from u µ o Ÿ ‰ Œ } •] • v • d u µ ô ò ó Ã • Z X] P] Z v] } ( ] v š Œ • ‰] v s] . Œ Ÿ v } v • ‰] Y Œ } v š • ~ µ • š ^ Z o µ î s í Œ • Œ Œ v œ š] u ž] • š } Œ Ç } (P o] Ç o o] ~ v P X P X Á Ù ô õ õ • X } u u } v } • Œ À Ÿ • š Z š Æ } v } u]] À Œ] •] š Œ } ‰] systems is characterized by an excessive number of geographically restricted and low abundant species, a ‰ © Œ] v µ u v š š o • (š Œ Œ ~ ; µ î ò ó ï V ^ š P š o X î ì í ï • X / v š Z] • š µ Á Ù v À • Ÿ P š ž ‰ © Œ (À • Œ] Ÿ } • v] š Á • Œ o } š] v u] • š ‰ Ç Œ] ( ] v] À Œ •] š Ç Œ Œ] š Œ Ç } Ç ‰ o v š u µ v] Ÿ • š Z] • o v ~ d Œ v Œ Z µ v] } w • u] Æ š µ Œ Á] š Z] w š Á š v Z Œ] • Ÿ v } š v] • o v ~ ì š Z š u ‰ Œ • œ] (d Œ ~] Œ } Œ ~ ì š Z • µ š Œ } ‰] • o] (d v Œ ~] (v Œ] v • š Z ~ ï š Œ } ‰] • o v } (Z µ v] } v D • Œ d Z • • š Z Œ] • o v • v } v •] Œ Œ ‰ Œ •] (š] + À Œ P v š P Œ ‰ Z]] • « v P Á •] š Z v š Œ • Ÿ] v P š d • Œ Œ] • Œ Ç } µ v P] • o ∀ ï X Ð í • o } v P š v š P Z š o v Œ Ž] ‰ o P } (š Z ì } Œ ~ u Ø X Ð • Á] š o Z } Z Œ] š] š À Œ •] š Ç ~ } Œ P v • } Œ š ì ò õ Ù Œ] v š Y o î X í î • d X v Œ] ( ] • v } o] Œ o ∀ í Ð • o • ‰ Œ { š v } š Z š Œ o v Ÿ Œ Z] ‰ ~ d š Z P] v Œ] Á •] š Z o } v P P Œ } o } P] o Z] • š } Œ Ç Œ Ð • v Z] P Z À Œ • ( ] š o Ç u š o • •] . Ÿ } • v Ð } v š } Ç r o š v o î X í ò •] Z • a high biological diversity and is a biodiversity hotspot in the Macaronesian region (Fernández-Palacios and Q Z] © l î Œ ì ô • & X] v o Z o Ç U] } ~ v ì X Ð • o } v P • š } š Z Ð • Œ / • o v ~ u Æ Œ Ð • U š Œ } ‰] o Z] ‰ archipelago located in the southwestern Indian Ocean known for its high level of diversity (Thébaud et al. ì ì õ U] Œ š o î X í ì • d Z • š Z Œ] • o v A • Œ sampled using the same methods, giving us the unique } ‰ ‰ } Œ š (µ] w] À š Ç Ÿ P Á Ÿ Z v P S Z š Z Œ } • Œ À ‰ © Œ v v) • u u µ v] • š š Œ Œ µ š Œ Œ Œ v •] • š Á v] š Z o } ‰ o © Œ (v À • Œ] Ÿ v] ‰ o v] À Œ •] Ÿ š Œ U ~ í š Z • š ‰] • • u o P v • Œ] v] À Œ (Œ š } Q Œ Œ ì ì ñ • v ~ î š Z š Z] v G µ v] (Œ Œ P ‰] } v taxonomic diversity increases from temperate to tropical Œ P] } v µ î ò ó ï U š P š o î X í ï • d X } Œ • • š Z • × µ • Ÿ } v Á • U v o Ç • v } u ‰ Œ À Œ o u ‰ } Œ š • v Œ] ‰ (š } Œ u µ v] • š š Œ Œ µ š µ ú Œ Z W } µ ‰ v Ç r (Œ] •] š Œ Z] Ç u Ÿ K } & • • v • ~ î š Z • ‰] • r µ v] v š Œ] µ Ÿ } v ð }] v À • Ÿ P š š Á } Œ ù (Œ Œ] š X Ç V X U v v µ v v • V ~ ï š Z v • š • ‰] • r Œ Œ o Ÿ } v •] Z v] À ‰ • Ÿ P š š Z • ‰ Ÿ • o o] v (P Œ Œ] v š Ç ô ò Z ‰ Œ Ÿ Ÿ } v] v P of beta diversity using a distance-decay framework to š • š (} Œ • ‰ Ÿ o ‰ © Œ v •] v } u u µ v] š

Methods

Field data collection

E Ÿ À Á U š U v o Œ P µ v o Ç • š µ Œ } Œ • Œ š • across the three study islands were selected. Study] • v } š Á • Œ o } š] v u } • š ‰ Ç Œ] (Ÿ Œ } v š Á } ( ] v] À Œ •] š Ç Œ Œ] š Œ Ç } Ç ‰ o v š u ‰ Œ • œ] (d Œ ~] Œ } Œ ~ ì š Z • µ š Œ } ‰] • o] (d v Œ ~] (v Œ] v • š Z ~ ï š Œ } ‰] • o v } (Z µ v] } v D • Œ d Z • • š Z Œ] • o v • v } v •] Œ Œ ‰ Œ •] (š] + À Œ P v š P Œ ‰ Z]] laurel forest sites in Tenerife. They are dominated by the woody plants *Ilex perado* subsp. *azorica*, *Juniperus brevifloraLaurus azorica*, *Myrsine africana*, and *Vaccinium cylindraceum*] v d Œ Œ] Œ Œ a v *borea*, *Erica*

platycodon, Ilex canariensis, Laurus novocanariensis, Morella faya, Prunus lusitanica, and Viburnum rigidum, and *Allophylo-Buxetum* (*Allophylus spicatus*, *Buxus vahalii*, *Heberdenia excelsa*, *Ocotea foetens*, *Picconia excelsa*, *Rhamnus crenulata*, *Teline canariensis*, *Visnea mocanera*) in Madeira, and Fayo-Perseetum (*Apollonias barbujana*, *Clethra arborea*, *Erica arborea*, *Ilex canariensis*, *Laurus novocanariensis*, *Morella faya*, *Prunus lusitanica*, and *Viburnum rigidum*), Mayteno-Ilicetum (*Allophylus spicatus*, *Bystropogon canariensis*, *Ilex canariensis*, *Maytenus umbellata*, *Myrica rivas-martinezii*, *Rhamnus crenulata*, *Viburnum rigidum*), Pruno-Lauretum (*Apollonias barbujana*, *Ilex canariensis*, *Laurus novocanariensis*, *Prunus lusitanica*, *Rhamnus crenulata*, *Viburnum rigidum*), Rhamno-Prunetum (*Ilex canariensis*, *Prunus lusitanica*, *Rhamnus crenulata*, *Viburnum rigidum*), and Sideritido-Ericetum (*Adenocarpus viscosus*, *Bystropogon canariensis*, *Calluna vulgaris*, *Chamaecytisus proliferus*, *Erica arborea*, *Erica scoparia*, *Ilex canariensis*, *Myrica faya*, *Pterocephalus lasiospermus*, *Rhamnus crenulata*, *Salvia canariensis*, *Teline canariensis*, *Viburnum rigidum*) in Tenerife. Finally, Aeonio-Euphorbietum (*Aeonium arboreum*, *Aeonium canariense*, *Aeonium urbicum*, *Euphorbia canariensis*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Asparago-Rhamnetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rhamnus crenulata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Asparago-Tamaricetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Euphorbio-Periplocetum (*Aeonium arboreum*, *Aeonium canariense*, *Aeonium urbicum*, *Euphorbia canariensis*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Kleinio-Euphorbietum (*Aeonium arboreum*, *Aeonium canariense*, *Aeonium urbicum*, *Euphorbia canariensis*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Periploco-Euphorbietum (*Aeonium arboreum*, *Aeonium canariense*, *Aeonium urbicum*, *Euphorbia canariensis*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Periploco-Rhamnetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rhamnus crenulata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Rhamno-Periplocetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rhamnus crenulata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), Rhamno-Tamaricetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rhamnus crenulata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*), and Tamarico-Periplocetum (*Asparagus arborescens*, *Asparagus umbellatus*, *Bupleurum salicifolium*, *Globularia salicina*, *Kleinia neriifolia*, *Periploca laevigata*, *Rubia fruticosa*, *Salvia canariensis*, *Schizogyne sericea*, *Sonchus acaulis*, *Tamarix canariensis*) in Reunion.

Ten 50 m × 50 m square plots were established on islands with at least 5 km between plots within the same mountain chain or 10 km between plots in different mountain chains. This size considered adequate to obtain measures of beta diversity that are independent of gamma diversity for tree communities (Condit et al. 2002). Four 5 m × 5 m square subplots were also delimited in which we counted all woody species shoots with a diameter at breast height (dbh) ≥ 1 cm and ≤ 10 cm. Plot and subplot sizes were chosen to maximize the number of species recorded in the plots, while minimizing the number of species recorded in the subplots.

Data analyses

All analyses were implemented in R version 3.1.0 (R Core Team 2014). We first calculated the minimum and maximum number of species per plot and subplot. These analyses were restricted to indigenous species (i.e., endemics plus natives) because the overall abundance.

We considered two forms of rarity: incidence (species occupancy) and abundance. To study incidence-based rarity, the occurrence of each species in each island was recorded. Species incidences within an island were measured as the number of plots where a species was recorded. Species incidences within an island were measured as the number of plots where a species was recorded.

To study abundance-based rarity, we focused on the most abundant to the least abundant species. and compared the following SAD models: the geometric series, the log-series, the Poisson lognormal, and the gambin model (Matthews et al. 2014). These models describe different aspects of the niche hypervolumes (measured by species abundance) of the most abundant to the least abundant species. Among all proposed SAD models, the geometric series, the log-series, the Poisson lognormal, and the gambin model (Matthews et al. 2014). These models describe different aspects of the niche hypervolumes (measured by species abundance) of the most abundant to the least abundant species. Among all proposed SAD models, the geometric

The lognormal is one of the most commonly used models in ecology (Ugland et al. 2007, Matthews et al. 2014). It assumes that the logarithmic abundances are distributed normally. In the gambin model, based on the gamma

normal at a log scale of abundance (Ugland et al. 2007, Matthews et al. 2014).

Two main methods were employed to plot and model the species' abundances in which data were binned in octaves (Preston 1948). In these plots, rank one corresponds to the species with the highest abundance, rank two corresponding to the species with the second highest abundance, and so on. As a method to determine the best SAD model for any given curves indicate lower evenness. The rank-abundance geometric series because if a log scale is used for abundance, the species fall exactly along a straight $\log a = \log b_0 + r \log b$, where a is the species abundance, r is the species rank, and $b_0 = 1 - b$. The geometric series model is the most uneven model and it is possible to use the regression slope to compare modelled the geometric series using un-binned "species rank abundance plots". However, the three datasets cannot be directly compared because they exhibit size (Borda-de-Água et al. 2011). To overcome this problem, we randomly sampled a number of 715 individuals, which corresponds to the minimum number of individuals in Tenerife. An OLS comparison between islands. Regression comparisons were assessed by performing an overall analysis of values using the R package multcomp (Hothorn et al. with the lowest AIC value was considered the best binned data. Bins were constructed using base 2. values of the lowest AIC were considered to have equivalent as sampling units. Our nested SARs are similar to the

of beta diversity in Reunion, which can impact on the value of the slope, led us to restrict the analyses for Reunion to only four plots located within a 12 km range, similar to the range covered by the 10 plots in Terceira and Tenerife. Thus, when we compared the slopes between the three islands, we avoided between plots in Reunion. The ten plots in Reunion (distances between individuals collected in the same observed distances were compared with 999 null distributed among the ten studied sites on each island. the observed average distance was below the 0.025 and abundance data.

regressed against the geographical distance between distance due to either a decrease in environmental similarity or by limits to dispersal and niche width differences among species (Nekola and White that beta diversity measures should be correlated diversity with interplot geographical distances. diversity and geographical distances was tested with Mantel tests using the R package vegan (Oksanen et and distance was tested using the R Package simba

Results

Alpha, beta and gamma diversity patterns

93 woody plant species were sampled across thirty Tenerife had very similar values of average alpha diversity

the other two islands. Beta diversity in Reunion was than Tenerife. The density of woody plants in Terceira gamma diversity in Terceira were the lowest of the

Table 1. Diversity metrics for woody vascular plants is the accumulated total number of species in the ten plots. Alpha is the mean number of species in the ten plots. Max and Min alpha is the maximum and minimum number of species found in the ten plots, respectively. N is the number of individuals.

	Terceira	Tenerife	Reunion
N	2186	715	1497
Gamma	11	17	67
Alpha	7.3	7.4	25.6
Beta	0.51	1.16	1.61
Max alpha	9	9	33
Min alpha	5	5	16

Rarity

of wood plant rarity. In Terceira, only 18% of woody plant species occur in one plot whilst 45% occur in all ten plots (Tokeshi test P_{righ} A ì X ì ì î followed, with 25% of the plant species occurring in only one plot and 3% occurring in all 10 plots (Tokeshi test $P_{o\ L}$ D ì X ì ì ì í

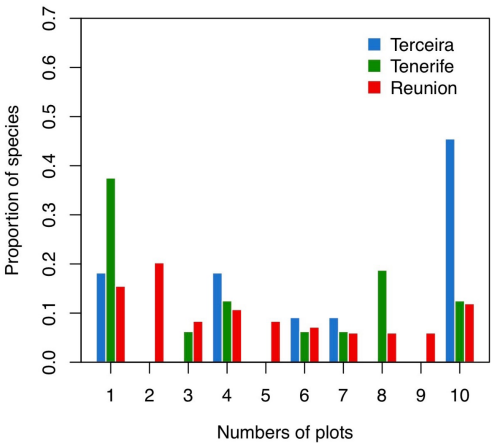

Figure 1. &

Tenerife and Reunion binned datasets whereas rank-abundance approach, the SADs for Terceira and Tenerife were characterised by steep curves (with z= -0.304 and the SAD for Reunion displayed a shallower curve (with z slopes:

Table 2. three SAD models (logseries, Poisson lognormal-PLN, and model is highlighted in bold. Gambin's alpha parameter

	Terceira	Tenerife	Reunion
Logseries	67.69	88.59	317.64
PLN	64.54	76	277.66
Gambin	**65.46**	**75.31**	**274.36**
Alpha	13.41	6.67	2.24

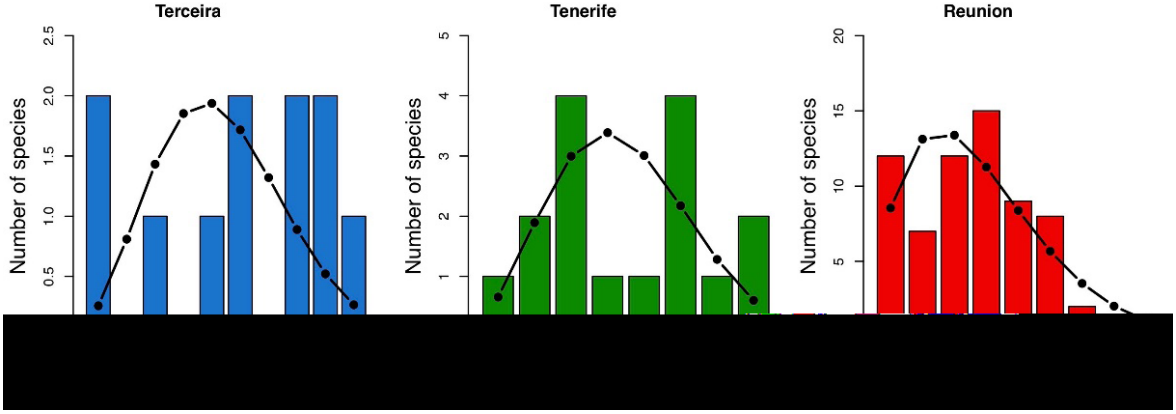

Figure 2. The following binning system was used: 0 corresponds to the number of species with 1 individual per species, bin 1 corresponds to the number of species with 2-3 individuals per species, bin 2 corresponds to the number of species

Species Area Relationships

The analyses of nested SARs confirmed the rapidly as sampling area increases in the two islands with the highest species richness (higher compared to the species poor and temperate island comparisons

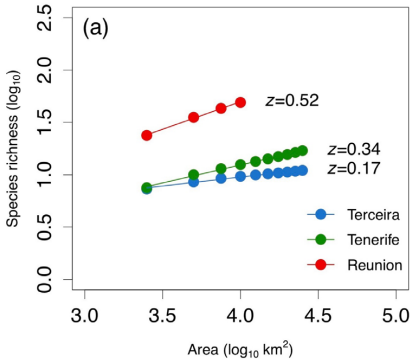

Figure 3. Geometric series rank-abundance plots for woody number of individuals as in the island with a lower overall values: Terceira y=-0.304x + 2.999, R² = 0.960.

Figure 4.

Spatial distribution

Z] P‰ Œ } ‰ }}Œ• ‰} vŸ dPdPÇŒE P• %‰] •(}µ v š Z îšð 9}(] v À • Ÿ P šu u µ v] ŸZ • were found in Terceira whereas overdispersion was found in Reunion. Distance decay was found in Terceira and Reunion, mostly driven by species replacement in both cases (Table 3). All Terceira plots were placed in Juniperus-Ilex forests, which are now the dominant natural forests of the island (Elias et al. 2015). The GFD for the woody plants at this small scale is also bimodal OFDs.

The Azorean woody plants showed an uncommon right-skewed unimodal shape, which is the most common shape found in other archipelagos (Borges et al. 2018). This shape can be generated by two possible, mutually non-exclusive, processes: (1) species have a low probability of being recorded at any one sampling unit (plots in this case); and (2) species are rare (Fig. 3). Species adapted to other habitats tend to occupy only a few plots in the woody habitat (Fig. 3).

Table 3. Ecological distance decay (Sørensen dissimilarity) for woody plants in Terceira, Tenerife and Reunion islands, using presence-absence and abundance data.

	Terceira	Tenerife	Reunion
Presence-absence data			
Intercept	0.9	0.9	0.9
Slope	0	0	0
Abundance data			
Intercept	0.9	0.9	0.9
Slope	0	0	0

Table 4. Beta-diversity values (Sørensen dissimilarity) and its components for woody plants in Terceira, Tenerife and Reunion islands, using standardized forests across different oceanic archipelagoes

	Terceira	Tenerife	Reunion
Btotal	0.00764*	0.00242	0.00316*
Brepl	0.01091*	-0.00090	0.00400*
Brich	-0.00330	0.00334	-0.00080

Discussion

According to Raunkiaer's law, occupancy frequency in the temperate island of Terceira are species poor and are dominated by widespread taxa whereas the tropical island of Reunion is richer and with only a few species that can be considered common.

According to Raunkiaer's law, occupancy frequency species in a community are either rare or common within a given island, if sampled plots exist within a variable environmental matrix where interplot distances

Because z-values in SACs are a measure of species replacement, highly isolated areas tend to share fewer species and, hence, have higher z values than within each island, we should expect shallower slopes (z) in classical nested SARs that use true isolates (Rosenzweig 1995). This was observed for Terceira plots, which was the shallowest slope among the three analysed islands, is in line with the z-value found for the Terceira plots is also consistent with the widespread

The other two SACs exhibit z values close to those with narrow environmental tolerances and limited within a given island, if sampled plots exist within a variable environmental matrix where interplot distances The very high z-value for Reunion, coupled with the

observed OFD, suggests the occurrence of many geographically structured. This may result from the for tropical systems and further exacerbated by the fact that sampling areas are ecologically uniform heterogeneity in our transect. The high z-value for Tenerife may be explained by the presence of both very rare species and species that are rare in the sampled plots because they are more strictly associated with other unsampled habitat types.

Regarding our SAD analyses, it is well known that the trees follow a logseries SAD. Our data for the tropical may be related to the fact that we were dealing with approximately 8% of woody species make up 50% of individual trees, and the SAD follows an approximate of hyper-dominance and an excess of rare species were best approximated by models that have more this island.

Regarding the gambin model, communities dominated by rare species are expected to have low as in the case of Terceira. In contrast, Tenerife, which has a few more species and lower impact of the most dominant ones, has an intermediate value of in richness. This means that, overall, the more distant

within an island. On the contrary, in Tenerife we did

diversity and distance, which may be a consequence of the complex orography of Anaga.

Colorado Island the nine most abundant species, out of tree species in the Amazon account for half of all explained by factors such as disturbance regimes, species destroyed, which probably contributed to some species forests in the Azores.

in the woody plant community structure of the regionally two regionally highly diverse islands (Tenerife and and Reunion is a consequence of comparably long species-poor biota of the Azores, constrained by recent geological history and low environmental diversity.

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The field research station of Mare Longue ~ WXKXµvX]}vXìî•v K^hZ µv]‰vŒ}À] o}P]•µ‰‰šZšµ Zµv]dvZE Ÿ}vo Park of Terceira and the Cabildo of Tenerife as well •šZZ µv]Ev Ÿ}vWoŒ‰ŒE}À‰ Œu(]šE• •‰]u}voo Ÿ]ÿ‰Œ}š Œ •]X]À Œ•]šÇ Monitoring of permanent plots at Reunion island has been cofunded by FEDER DIVINES (1.02 Région Z µv]}v îìíñ•X

PAVB, PC, BCE, CT, PO, DS, RBE, JMFP and JCC conceived the study design and sampling program. RBE, AJP, JMFP, RO, SFL, LN, JCC, AMS and DS performed ‰o•vš‰o]wP vŸ. ŸWWW s&LZ^U&U U dD v oÇšZ šWW sWU v ^&o šZÁŒ]Ÿv P with the help of FR, LDB, LBD, TM, IRA, MF, JCC, RBE, JMFP, PO, CT, DS, BCE. All authors commented on the .v o À Œ•]}v }(šZ u vµ• Œ]‰šX

References

Baider, C., Florens, F.B.V., Bare, S., Beaver, K., Matatiken, D., Strasberg, D. & Kueffer, C. (2010) Status of plant conservation in oceanic islands of the Western Indian Ocean. Proceedings of the 4th Global Botanic Gardens Congress, pp. 1–7. Digital resource available at www.bgci.org/resources/2484

Barreto, S., Borges, P.A.V. & Guo, Q. (2003) A typing error in the Tokeshi´s test of bimodality. Global Ecology and Biogeography, 12, 173–174.

Borda-de-Água, L., Whittaker, R., Cardoso, P., et al. (2017) Dispersal ability determines the scaling properties of species abundance distributions: a case study using arthropods from the Azores. Scientific Reports, 7, 3899.

Borges, P.A.V., Cardoso, P., Cunha, R., et al. (2011) Macroecological patterns of species distribution, composition and richness of the Azorean terrestrial biota. Ecologi@, 1, 22–35.

Borges, P.A.V., Cardoso, P., Kreft, H., et al. (2018) A Global Island Monitoring Scheme (GIMS) for the long-term coordinated survey and monitoring of forest biota across islands. Biodiversity and Conservation, 27, 2567–2586.

Borges, P.A.V. & Hortal, J. (2009) Time, area and isolation: factors driving the diversification of Azorean arthropods. Journal of Biogeography, 36, 178–191.

Brown, J. (2014) Why are there so many species in the tropics? Journal of Biogeography, 41, 8–22.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multi-model inference: a practical information theoretic approach. 2nd edn. Springer, New-York

Cardoso, P., Rigal, F. & Carvalho, J.C. (2015) BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods in Ecology and Evolution, 6, 232–236.

Carine, M.A. & Schaefer, H. (2010) The Azores diversity enigma: why are there so few Azorean endemic flowering plants and why are they so widespread?. Journal of Biogeography, 37, 77–89.

Carvalho, J.C., Cardoso, P. & Gomes, P. (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography, 21, 760–771.

Chao, A., Colwell, R.K., Lin, C.W. & Gotelli, N.J. (2009) Sufficient sampling for asymptotic minimum species richness estimators. Ecology, 90, 1125–1133.

Colwell, R. K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Digital resource available at http://purl.oclc.org/estimates .

Elias, R.B., Dias, E. & Pereira, F. (2011) Disturbance, regeneration and the spatial pattern of tree species in Azorean mountain forests. Community Ecology, 12, 23–30.

Elias, R.B., Gil, A., Silva, L., Fernández-Palacios, J.M., Azevedo, E.B. & Reis, F. (2016) Natural zonal vegetation of the Azores Islands: characterization and potential distribution. Phytocoenologia, 46, 107-123.

Fattorini, S. (2005) A simple method to fit geometric series and broken stick models in community ecology and island biogeography. Acta Oecologica - International Journal of Ecology, 28, 199–205.

Fattorini, S., Borges, P.A.V., Dapporto, L. & Strona, G. (2017) What can the parameters of the species-area relationship (SAR) tell us? Insights from the Mediterranean islands. Journal of Biogeography, 44, 1018–1028.

Fattorini, S., Cardoso, P., Rigal, F. & Borges, P.A.V. (2016) Using species abundance distribution models and diversity indices for biogeographical analyses. Acta Oecologica - International Journal of Ecology, 70, 21–28.

Fernández-Palacios, J.M. & Whittaker, R.J. (2008) The Canaries: An important biogeographical

meeting place. Journal of Biogeography, 35, 379–387.

Gaston, K.J. (1994) Rarity. Chapman, Hall, London.

Grøtan, V. & Engen, S. (2009) poilog: Poisson lognormal and bivariate Poisson lognormal distribution. R package ver. 0.4. Digital resource available at https://CRAN.R-project.org/package=poilog

Harte, J., Smith, A.B. & Storch, D. (2009) Biodiversity scales from plots to biomes with a universal species-area curve. Ecology Letters, 12, 789–797.

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society of London, 68, 87-112.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.A., Schuetzenmeister, A. & Scheibe, S. (2017) Simultaneous inference in general parametric models. Digital resource available at https://CRAN.R-project.org/package=multcomp

Hubbell, S.P. (2013) Tropical rain forest conservation and the twin challenges of diversity and rarity. Ecology and Evolution, 3, 3263–3274.

Hui, C. (2012). Scale effect and bimodality in the frequency distribution of species occupancy. Community Ecology, 13, 30–35.

Jurasinski, G. & Retzer, V. (2012) Simba: a collection of functions for similarity analysis of vegetation data. R package version 0.3-5. Digital resource available at http://CRAN.R-project.org/package=simba

Legendre, P. (2014) Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography, 23, 1324–1334.

Magurran, A.E. (2004) Measuring Biological Diversity. Blackwell Publishing, London.

Matthews, T.J., Borregaard, M.K., Ugland, K., Borges, P.A.V., Rigal, F., Cardoso, P. & Whittaker, R.J. (2014) The gambin model provides a superior fit to species abundance distributions with a single free parameter: evidence, implementation and interpretation. Ecography, 37, 1002–1011.

Matthews, T.J., Triantis, K.A., Rigal, F., Borregaard, M.K., Guilhaumon, F. & Whittaker, R.J. (2016) Island species–area relationships and species accumulation curves are not equivalent: an analysis of habitat island datasets. Global Ecology and Biogeography, 25, 607–618.

Matthews, T.J. & Whittaker, R.J. (2014) Fitting and comparing competing models of the species abundance distribution: assessment and prospect. Frontiers of Biogeography, 6, 67–82.

McGill, B.J. (2003) A test of the unified neutral theory of biodiversity. Nature, 422, 881–885.

Montoya-Alonso, J.A., Carretón, E., Morchón, R., Silveira-Viera, L., Falcón, Y. & Simón, F. (2016) The impact of the climate on the epidemiology of *Dirofilaria immitis* in the pet population of the Canary Islands. Veterinry Parasitology, 30, 66–71.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. Journal of Biogeography, 26, 867–878.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) Vegan: Community Ecology Package. R package version 2.2-1. Digital resource available at http://CRAN.R-project.org/package=vegan

Papp, L. & Izsák, J. (1997) Bimodality in occurrence classes: a direct consequence of lognormal or logarithmic series distribution of abundances: a numerical experimentation. Oikos, 79, 191–194.

R Development Core Team (2015) R: A Language and Environment for Statistical Computing v3.1.3. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. Digital resource available athttp://www.R-project.org .

Rosenzweig, M.L. (1995) Species diversity in space and time. Cambridge University Press, Cambridge.

Schaefer, H. (2003) Chorology and diversity of the Azorean flora. Dissertationes Botanicae, 374, 1–130.

Scheiner, M. (2003) Six types of species–area curves. Global Ecology and Biogeography, 12, 441–447.

Schluter, D. (2016) Speciation, ecological opportunity, and latitude. The American Naturalist, 187, 1-18.

Sjøgren, E. (1973) Recent changes in the vascular flora and vegetation of the Azores Islands. Memórias da Sociedade Broteriana, 22, 1–451.

Solé, R.V., Alonso, D. & Saldaña, J. (2004) Habitat fragmentation and biodiversity collapse in neutral communities. Ecological Complexity, 1, 65–75.

ter Steege, H., Pitman, N.C.A., Sabatier, D. et al. (2013) Hyper-dominance in the Amazonian tree flora. Science 342, 325–334.

Thébaud, C., Warren, B.H., Cheke, A.C. & Strasberg, D. (2009) Mascarene Islands, Biology. In: Encyclopedia of Islands (ed. by R.G. Gillespie and D. Clague), pp. 612–619. University of of California Press, Berkeley, USA.

Tokeshi, M. (1992) Dynamics and distribution in animal communities; theory and analysis. Research in Population Ecology, 34, 249–273. doi:10.1007/BF02514796

Triantis, K., Hortal, J., Amorim, I.R., Cardoso, P., Santos, A.M.C., Gabriel, R. & Borges, P.A.V. (2012) Resolving the Azorean knot: a response to Carine, Schaefer (2010). Journal of Biogeography, 39, 1179–1184.

Ugland, K.I., Lambshead, F.J.D., McGill, B.J., Gray, J.S., O'Dea, N., Ladle, R.J. & Whittaker, R.J. (2007) Modelling dimensionality in species abundance distributions: description and evaluation of the Gambin model. Evolutionary Ecology Research, 9, 313–324.

Ulrich, W., Kusumoto, B., Shiono, T. & Kubota, Y. (2016) Climatic and geographical correlates of global forest tree species abundance distributions and community evenness. Journal of Vegetation Science, 27, 295–305.

Xu, W., Chen, G., Liu, C. & Ma, K. (2015) Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. Global Ecology and Biogeography, 24, 1170–1180.

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Supporting Information

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Appendix S1 – /v(}Œu Ÿ}v }µš šZ •]š •

Appendix S2 - Dataset.

